

AMERICAN MUSEUM *Novitates*

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, N.Y. 10024
Number 3159, 29 pp., 13 figures, 3 tables February 15, 1996

Biting Midges from Upper Cretaceous New Jersey Amber (Ceratopogonidae: Diptera)¹

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ABSTRACT

Nine species of Ceratopogonidae are recognized in Turonian New Jersey amber (88–93.5 million years old), based on 20 specimens: *Leptoconops copiosus*, n. sp., *Leptoconops curvachelus*, n. sp., *Alautunmyia elongata*, n. g., n. sp., *Atriculicoides globosus* (Boesel), *Heleageron grimaldii*, n. sp., *Culicoides casei* Grogan and Szadziewski, *Culicoides bifidus*, n. sp., *Culicoides grandibocus*, n. sp., and *Palaeobrachypogon remmi* Borkent. *Atriculicoides globosus* (Boesel) and *Palaeobrachypogon remmi* Borkent are also present in slightly younger Canadian amber (71–84 million years old).

Phylogenetic analysis indicates that all these New

Jersey species represent early lineages within the family. There is no evidence of extinction of Cretaceous lineages of Ceratopogonidae (all fossils exhibit only plesiomorphic features).

The presence of a species with palisade setae suggests that some Ceratopogonidae have preyed on other Nematocera for at least the past 88–93.5 million years. The mouthpart structure of female *Culicoides grandibocus* suggests that these probably fed on the blood of dinosaurs. The prevalence of members of *Leptoconops* (10 specimens) indicates that saline beaches were likely a common habitat in New Jersey during the Turonian.

INTRODUCTION

The Ceratopogonidae are quickly becoming an exemplary group for interpreting past patterns of diversification. The overall cladistic relationships of major lineages have

been interpreted by Borkent (1995) and Szadziewski (1988) and, as further supported by this paper, the group has a remarkable and detailed fossil record in the Northern Hemi-

¹ Paleontology of New Jersey amber, Part IV.

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sphere. Ceratopogonidae are known from virtually every amber deposit from which insects have been recorded and are one of the most common groups represented within those ambers. Many of these Tertiary and Cretaceous fossils have been described in detail by Borkent (1995; Canadian amber—71–84 mya), Borkent and Bissett (1990; Rott compressions—23–30 mya, Baltic amber—30–55 mya); Grogan and Szadziwski (1988; New Jersey amber—88–93.5 mya), Hong (1981; Fushun amber—36–57 mya), Remm (1976; Taimyr amber—83–89 mya), Szadziwski (1988; Baltic amber—30–55 mya), Szadziwski (1990a; Sakhalin amber—36–65 mya), Szadziwski (1993; Saxonian amber—22 mya), Szadziwski and Grogan (1994a, 1994b; Dominican amber—20–30 mya) and Szadziwski and Schlüter (1992; French amber—93–99 mya). Further studies are currently underway to interpret remaining collections, especially from the Dominican Republic, the Taimyr Peninsula in Russia, and from Lebanon. Analysis of these fossils in the light of cladistic relationships indicates that there is an excellent correspondence between phylogenetic patterns and the age of the fossils being described: successively older fossils belong only to successively older phylogenetic lineages (Borkent, 1995).

The current paper describes nine species of Ceratopogonidae based on a total of 20 specimens present in New Jersey amber, all of Turonian age and therefore 88–93.5 million years old (Obradovich, 1993). Previous papers discussing this amber (Borkent, 1995; Grimaldi et al., 1989; Grogan and Szadziwski, 1988) have assumed that Sayreville amber originated below the South Amboy Fire Clay and hence was Cenomanian in age. In fact, the amber was found just above the South Amboy Fire Clay (Grimaldi, personal commun.); this stratigraphic position and palynological analyses by Christopher (1977, 1979) indicate that the amber is of Turonian age.

One species of biting midge, *Culicoides casei* Grogan and Szadziwski, 1988, was previously described from this amber, was subsequently redescribed by Borkent (1995: 66), and is further redescribed here because of the discovery of two more specimens. Together with those species described by Szadziwski and Schlüter (1992) from the slightly

older Upper Cretaceous French amber (Cenomanian in age), these are among the oldest Ceratopogonidae that have been described (Current studies of Ceratopogonidae in Lebanese amber, about 127–130 million years old are under way by both this author and R. Szadziwski; a Lower Cretaceous specimen from Austria is also being studied by the author.) The recognition of the Lower Cretaceous (Aptian: 111–121 mya) “Simuliid? indet. 2” from Jell and Duncan (1986) as a possible *Austroconops* by Szadziwski (1990b) is probably incorrect. My study of the poorly preserved fossil indicates that it is more likely to be a male *Leptoconops*.

A variety of other insect families have been found in New Jersey amber, including 13 families of Diptera (mostly Nematocera) and a list of all included families will be published in the near future (Grimaldi, personal commun.). Of these insects, only a few have been described or analyzed in any detail: Apidae by Michener and Grimaldi (1988a, 1988b); Formicidae by Wilson et al. (1967a, 1967b) and Wilson (1985, 1987); and Sciaroidea by Grimaldi et al. (1989).

The list of fossils in New Jersey amber (Grimaldi, personal commun.) indicates that a wide array of habitats were present during the Turonian. The presence of immatures of Simuliidae certainly demonstrates the presence of running water and the occurrence of Chironomidae, Ephemeroptera, and Trichoptera further suggests that a variety of other aquatic habitats were available as well. The immatures of early lineages of extant Ceratopogonidae (Forcipomyiinae, Dasyhelinae, Culicoidini, many Ceratopogonini) live in small water bodies (e.g., tree holes, epiphytes, rock pools) or in the wet substrate found on the margins of streams, rivers, ponds, or marshes. Many other species are present in moist or wet decaying vegetation or manure. These microhabitats were likely the home for New Jersey amber ceratopogonids (also see below under species of *Leptoconops*, which likely bred in saline sand).

ACKNOWLEDGMENTS

David Grimaldi kindly arranged for the loan of the fascinating fossils described in this

paper and I thank him for his support and encouragement during the course of this study. He also took the photographs presented in figures 7 and 8. Raymond J. Pupedis graciously arranged for the loan of the type specimen of *Culicoides casei* from the Peabody Museum of Natural History, Yale University. The indefatigable collecting efforts of Gerard R. Case, James J. Leggett, and Paul D. Borodin are greatly appreciated.

My wife Annette, as usual, has supported this work with her love and finances. I express my sincere gratitude to her for her generous help.

I sincerely thank the following for their critical reviews of this paper: David Grimaldi, William L. Grogan, and Ryszard Szadziewski. Neal L. Evenhuis kindly checked to ensure that the name *Alautunmyia* had not been previously used. Jim Troubridge printed out the labels used in this study.

MATERIALS AND METHODS

The 20 amber specimens were prepared, examined, measured, and analyzed in the manner described by Borkent (1995). All specimens were mounted on microscope slides and are housed in the American Museum of Natural History, New York (AMNH), or in the case of *C. casei*, at the Peabody Museum of Natural History, Yale University, New Haven, Connecticut (PMNH). One additional specimen was in such poor condition as to be hardly identifiable as a Ceratopogonidae. It was not mounted or included in this study (AMNH no. NJ-49).

Specimens came from either White Oaks Pits, Sayreville, New Jersey (Grimaldi et al., 1989) or Sunrise Landing Site, E. Brunswick, approximately 6.5 km SW of Sayreville. Chemical analysis of amber from the Sunrise Landing Site indicates that it is indistinguishable from Sayreville amber (Grimaldi, personal commun.), indicating a common botanical origin and age. The presence of *Leptoconops curvachelus* in both amber deposits further indicates their contemporaneous age, as do several other insect inclusions like *Sphecomyrma* ants (Grimaldi, personal commun.).

KEY TO ADULT CERATOPOGONIDAE IN NEW JERSEY CRETACEOUS AMBER

1. Ommatidia broadly spaced dorsally (fig. 2G, H) 2
 Ommatidia narrowly spaced dorsally 4
2. Wing with radial veins compacted anteriorly (fig. 1A) 3
 – Wing with cells r_1 and r_{2+3} well-defined (fig. 2I) *Alautunmyia elongata*, n. sp.
3. Tarsomeres of all legs without well-defined armature; tarsal claws evenly curved from base to apex and with very small inner tooth (fig. 1M, N) *Leptoconops copiosus*, n. sp.
 – First and fifth tarsomere of each leg with thick setae (fig. 2C–E); tarsal claws with subapical bend and with large, thick inner tooth (fig. 2C–E) (male unknown) *Leptoconops curvachelus*, n. sp.
4. Ommatidia broadly abutting medially on dorsum of head capsule; wing entirely covered with macrotrichia *Atriculicoides globosus* (Boesel)
 – Ommatidia barely meeting medially on dorsum of head capsule; wing with, at most, scattered macrotrichia on wing membrane (fig. 4A, F) 5
5. First tarsomere of hindleg with well-defined row of palisade setae and thick basal spine (fig. 6C) *Palaeobrachypogon remmi* Borkent
 – First tarsomere of hindleg with scattered setae and lacking thick basal spine (fig. 4H) ... 6
6. One radial cell present, wing membrane lacking macrotrichia (fig. 3C) *Heleageron grimaldii*, n. sp.
 – Two radial cells present, wing membrane with at least a few macrotrichia on wing membrane (fig. 4A, F) 7
7. Mouthparts very long (fig. 5C) *Culicoides grandibocus*, n. sp.
 – Mouthparts short or of moderate length ... 8
8. Gonostylus narrowing gradually to pointed apex (fig. 4B, C) *Culicoides casei* Grogan and Szadziewski
 – Gonostylus thick for most of length, with outer indentation near middle length, apex bifid (fig. 5A, B) *Culicoides bifidus*, n. sp.

DESCRIPTION OF TAXA

***Leptoconops (Leptoconops)*
copiosus Borkent, new species**
 Figures 1A–O, 7A

DIAGNOSIS: *Male*. The only Cretaceous species of Ceratopogonidae with only the ter-

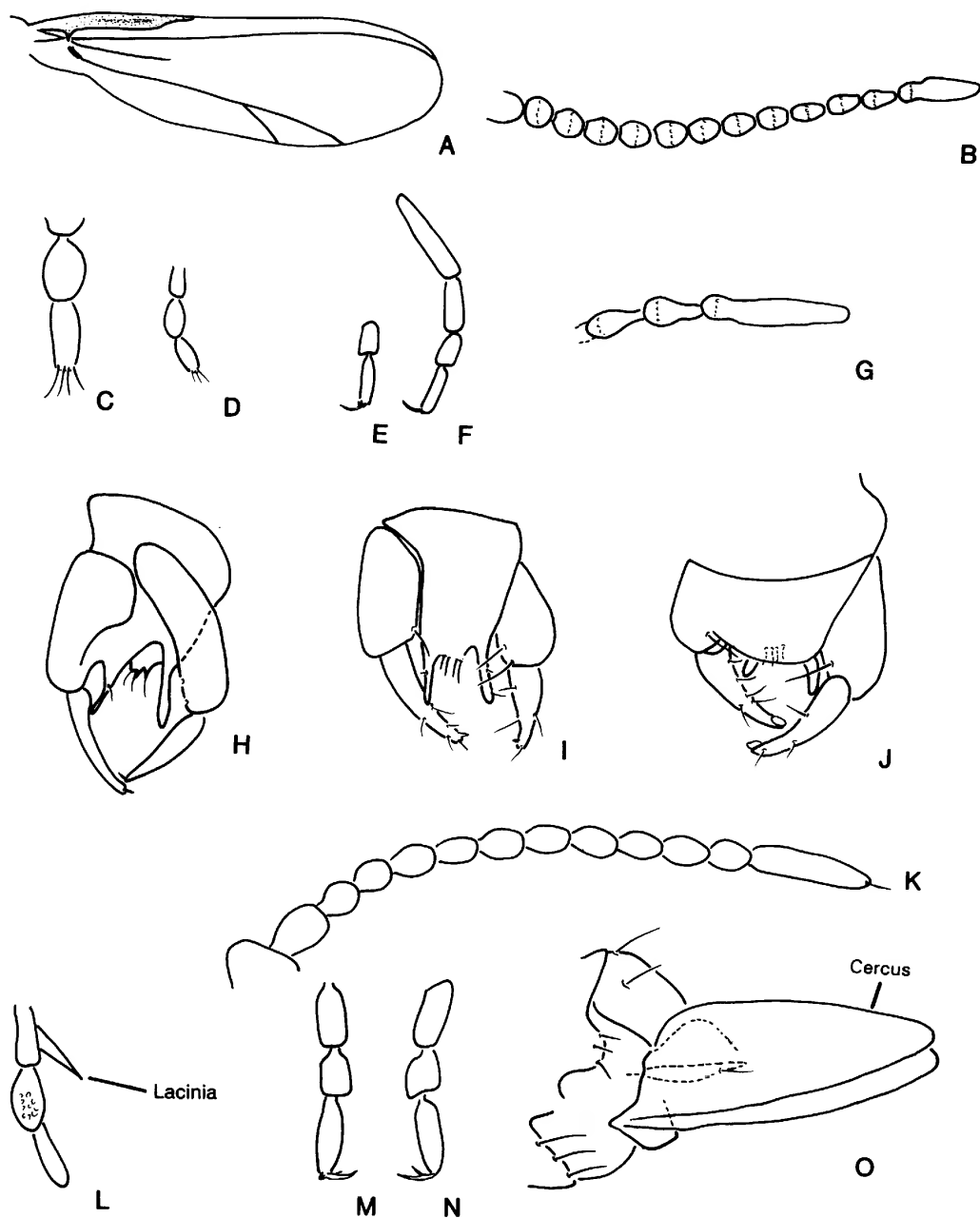


Fig. 1. Structures of *Leptoconops copiosus*. A-J male, K-O female. A. Wing (NJ-42, #2). B. Antenna (NJ-42, #2). C. Palp (NJ-41A, #2). D. Palp (NJ-42, #2). E. Tarsomeres 4-5 of midleg (NJ-42, #2). F. Tarsomeres 2-5 of hindleg (NJ-42, #2). G. Terminal flagellomeres of antenna (NJ-41A, #2). H. Genitalia (NJ-42, holotype). I. Genitalia (NJ-41A, #2). J. Genitalia (NJ-41A, #2). K. Antenna (NJ-42, allotype). L. Palp and apex of lacinia (NJ-42, allotype). M. Tarsomeres 3-5 of foreleg (NJ-42, allotype). N. Tarsomeres 3-5 of hindleg (NJ-42, allotype). O. Lateral view of genitalia (NJ-42, allotype).

minial flagellomere elongate and a wing length of less than 0.62 mm. *Female*. The only Cretaceous species of Ceratopogonidae with markedly elongate cerci somewhat pointed apically.

DESCRIPTION: Male adult. Head: Eyes bare, broadly separated dorsomedially. Vertex without single dorsomedial seta. Antenna with well-developed plume, basal foramen of pedicel not visible, 13 separate flagellomeres,

antennal ratio = 0.45–0.50 ($n = 3$), flagellomere 10/11 = 0.90–1.00 ($n = 3$), flagellomere 13 more elongate than preceding flagellomeres (fig. 1B, G). Mouthparts moderately elongate, mouthpart length/length of fifth tarsomere of foreleg = 1.69 ($n = 1$). Palp with four segments, third segment somewhat ovoid, with capitate sensilla not visible, palp segment $3/4 + 5 = 0.90$ –1.00 ($n = 3$) (fig. 1C, D). **Thorax:** Anterior scutal apodemes not visible. Scutum pruinose, with a few scattered elongate setae, humeral pit of moderate size. Anapleural suture elongate. Katepisternum with several setae. **Wing** (fig. 1A): Length = 0.57–0.62 mm ($n = 3$), costal ratio = 0.24–0.28 ($n = 3$). Without macrotrichia, fine microtrichia on all membrane. Alula without macrotrichia. Cells r_1 and r_{2+3} compacted anteriorly, not distinguishable. Base of M poorly defined, bifurcation not visible. **Legs:** Femora, tibiae slender. Legs lacking armature. Setae on fore- and midleg trochanter not visible. Midleg tibia with apical spur. Hindleg first tarsomere without thick basal spine, without palisade setae. Claws simple. With short empodium. **Genitalia** (fig. 1H–J): Apicolateral processes broadly separated, each elongate, slender, with apical seta. Gonocoxite moderately elongate. Gonostylus thick basally, tapering to toothed apical spine, lacking thick seta on outer face. Paramere not visible. Aedeagus not visible.

Female adult. Head: Eyes bare, broadly separated dorsomedially. Vertex without single dorsomedial seta. Antenna with 12 separate flagellomeres, antennal ratio = 0.69 ($n = 2$), terminal flagellomere more elongate than preceding flagellomeres (fig. 1K), first flagellomere sensilla not visible. Mouthparts moderately elongate, mouthpart length/length of fifth tarsomere of foreleg = 2.31 ($n = 1$). Clypeus separated laterally by membrane from head capsule. Labrum not visible. Mandible not clearly visible. Lacinia short, lacking teeth (fig. 1L). Palp with four segments, third segment somewhat ovoid, with capitate sensilla scattered on surface (fig. 1L), palp segment $3/4 + 5 = 1.00$ –1.10 ($n = 2$). Hypopharynx not visible. **Thorax:** Anterior scutal apodemes not visible. Scutum pruinose, with a few scattered elongate setae, humeral pit not visible. Anapleural suture elongate. Katepisternum with several setae. **Wing:** Length =

0.59 mm ($n = 1$), costal ratio = 0.35 ($n = 1$). Without macrotrichia, fine microtrichia present on all membrane. Alula without macrotrichia. Cells r_1 and r_{2+3} compacted anteriorly, not distinguishable. Base of M poorly defined, bifurcation not visible. **Legs:** Femora, tibiae slender. Legs lacking armature. Thick pair of setae on fore- and midleg trochanter absent. Hind first tarsomere without thick basal spine, without palisade setae. Foreleg, midleg, hindleg claws equal, simple, with very slender inner tooth arising from near base of each talon (fig. 1M, N). Hindleg claw shorter than fifth tarsomere. Claws of all legs of equal length, hind claw length/hind fifth tarsomere = 0.38 ($n = 2$). With short empodium. **Genitalia** (fig. 1O): Spermathecae not visible. Posterior margin of sternite 8 apparently with thick setae. Sternite 9 with lateral lobe bearing setae. Segment 10 with pair of setae (only one lateral seta visible). Cercus elongate, laterally compressed, somewhat tapering apically.

DISTRIBUTION AND BIONOMICS: *Leptoconops copiosus* is known from amber collected at Sunrise Landing Site, E. Brunswick, New Jersey.

As discussed by Borkent (1995), most species of extant *Leptoconops* are associated with sand or sandy soils, which include some salts and in which larvae burrow and feed. Furthermore, the elongate female cerci of some *Leptoconops* are likely related to laying eggs in sand. These features make it probable that *L. copiosus* was also associated with salty and sandy habitat. During the Turonian, New Jersey was, like today, on the edge of the continent and beach habitat was presumably prevalent in the area. The fact that 10 out of 19 ceratopogonid fossils in New Jersey amber were members of this genus suggests that the habitat was common in the area. Stratigraphy of the deposit further indicates that the amber, layers of sand and clay, and lignitic peat are stranded materials from an ancient, deltaic environment.

Female *L. copiosus* likely did not feed on any vertebrate as indicated by the presence of a reduced lacinia. All other Ceratopogonidae feeding on vertebrates have elongate laciniae with well-developed retrorse teeth (tables 2, 3; Borkent, 1995).

TAXONOMIC DISCUSSION: The two sexes

TABLE 1

Character States Used to Determine Relationships Presented in Figure 9.
Polarity decisions and further details are discussed by Borkent (1995).

No.	Character	Plesiomorphic	Apomorphic
1	Genital fork	Present	Absent
2	Larval pharyngeal apparatus	Absent	Present
3	Apicolateral process	Absent	Present
4	Divided larval body segments	Absent	Present
5	Thick radius	Absent	Present
6	Elongate female cercus	Absent	Present
7	3rd palp pit	Present	Absent
8	Gonostylus with apical spine	Present	Absent
9	Single vertex seta	Absent	Present
10	Strong postoccipital ridge	Absent	Present
11	Male claws bifid	Absent	Present
12	Midleg tibial spur	Present	Absent
13	Narrowly separated ommatidia	Absent	Present
14	Scutellum with 90° angle	Absent	Present
15	Long anapleural suture	Present	Absent
16	Fore, mid trochanter setae	Absent	Present
17'	Pedicel with moderate foramen	Absent	Present
17"	Pedicel with large foramen	Absent	Present
18	Ommatidia broadly abutting	Absent	Present
19	Female claws simple	Absent	Present
20	Larval setae on projections	Absent	Present
21	Last flagellomere with nipple	Absent	Present
22	Paratergite with setae	Absent	Present
23	Male flagellomere striated	Absent	Present
24	Scape with ventral apodeme	Absent	Present
25	Egg c-shaped	Absent	Present
26	Female sternite 9	Undivided	Divided
27	3 flagellomeres: sensilla coel.	Absent	Present
28'	Partial row of palisade setae	Absent	Present
28"	Complete row of palisade setae	Absent	Present
29	Aedeagus divided: four prongs	Absent	Present
30	Hind tibial spur	Present	Absent
31	Parameres overlapping	Absent	Present
32	Katepisternal setae	Absent	Present
33	Flagellomere 11 fused	Absent	Present
34	Female labium: setae on stalks	Absent	Present
35	Anepisternal setae	Absent	Present
36	Parameres	Present	Absent
37	Number of palp segments	5	2
38	Male scape with dorsal flange	Absent	Present
39	Aedeagus membranous medially	Absent	Present
40	Female abdominal 9, 10 elongate	Absent	Present
41	Female wing indented apically	Absent	Present
42	Male cerci large, long	Absent	Present
43	Hind femur with 2-4 rows spines	Absent	Present
44	Hind femur spines >0.58 femur	Absent	Present
45	Female clypeus fused with eye	Absent	Present
46	Female wing: costal extension	Absent	Present
47	Number of radial cells	2	1
48	Palp segments 4 + 5 fused	Absent	Present
49	Parameres fused into sphere	Absent	Present
50	Male segment 9 very large	Absent	Present

TABLE 1—(Continued)

No.	Character	Plesiomorphic	Apomorphic
51	Male forecoxa: many setae	Absent	Present
52'	3 scutal apodemes close	Absent	Present
52"	Scutal apodemes fused: 2	Absent	Present
53'	M ₁ , M ₂ forking at r-m	Absent	Present
53"	M ₁ , M ₂ forking before r-m	Absent	Present
54	Gonocoxites fused	Absent	Present

were associated through the presence of two males and one female in one piece of amber (AMNH no. NJ-41) and four males and one female in another piece (AMNH no. NJ-42).

Both pieces containing *L. copiosus* were cut into two (AMNH no. NJ-42) or three (AMNH no. NJ-41A, NJ-41B) parts to facilitate examination of the inclusions. Both pieces of amber were clear and free of contaminants.

The type specimens were generally in excellent condition, varying from completely opaque (fig. 7A) to partially decomposed (allowing for more detailed examination). However, one male paratype in piece NJ-42 was missing most of its thorax, some legs, and all of its head. One male paratype in piece NJ-41A was also in poor condition, distorted and missing some of its thorax, some legs, and part of the abdomen (including the apex).

The allotype female is shown in a photograph in Grimaldi (1993).

Because at present we have no synapomorphy indicating the monophyly of *Leptoconops* s. str. (Borkent, 1995), it may be that *L. copiosus* is more closely related to either *Megaconops* Wirth and Atchley or *Proleptoconops* Clastrier (fig. 10A). However, details of setation of the head and legs and the shape of the tarsal claws are consistent with the diagnosis of *Leptoconops* s. str.

Leptoconops copiosus is similar to *L. primaevus* from Canadian amber (Campanian). Their male genitalia are indistinguishable, although it should be noted that variation in angle of observation and varying states of preservation made it impossible to compare these in detail. At present, males of these two species can only be identified on the basis of wing length. Females of the two species differ in the shape of the cerci and, marginally, in a few meristic features (antennal ratio, palp segment 3/4 + 5, costal ratio). *Leptoconops*

copiosus is 4–22.5 million years older than *L. primaevus*.

TYPES: Holotype, male adult in amber on microscope slide, marked with an arrow on the coverslip, labeled “Holotype *Leptoconops copiosus* Borkent”, “Allotype *Leptoconops copiosus* Borkent”, “Paratypes *Leptoconops copiosus* Borkent: 3 males”, “AMBER: Late Cretaceous, New Jersey: E. Brunswick, Sunrise Landing Site, G.R. Case, coll. AMNH no. NJ-42” (AMNH); allotype, female adult in amber on same slide as holotype (AMNH); paratypes: 3 males in amber on same slide as holotype, labeled with no. 1, 2, 3 respectively (AMNH); 2 males, 1 female in amber (males on separate slide labeled AMNH no. NJ-41A and labeled no. 1, 2 respectively, female slide labeled AMNH no. NJ-41B), from type locality (AMNH).

DERIVATION OF SPECIFIC EPITHET: The name *copiosus* (abundant) refers to the prevalence of this species in New Jersey amber.

Leptoconops (Leptoconops) curvachelus Borkent, new species
Figures 2A–F, 7B–D

DIAGNOSIS: *Male.* Unknown. *Female.* The only Cretaceous species of Ceratopogonidae with tarsal claws with subapical bend.

DESCRIPTION: *Female adult.* **Head:** Eyes bare, broadly separated dorsomedially. Vertex without single dorsomedial seta. Antenna with 12 separate flagellomeres, antennal ratio = 0.65–0.76 (n = 2), terminal flagellomere more elongate than preceding flagellomeres (fig. 2A), first flagellomere sensilla not visible. Mouthparts moderately elongate, mouthpart length/length of fifth tarsomere of foreleg = 2.10 (n = 1), details of each mouthpart not visible. Clypeus separated laterally by membrane from head capsule. Palp with four seg-

TABLE 2
Relationship Between Feeding Habits of Families of Nematocera and Mouthpart Structure,
Exclusive of the Ceratopogonidae

Taxa closely related to Diptera are also included. Families are rearranged in a phyletic sequence based on Wood and Borkent (1989). FT = finely toothed. CT = coarsely toothed. SBI = sucking blood from invertebrates. SBV = sucking blood from vertebrates. NSB = not sucking blood. More than one entry for a given family is marked by an asterisk and indicates a variety of conditions present within that family. ? = uncertain status.

Taxon	Mouthparts					Feeding Mode		
	Mandible		Smooth —absent	Lacinia		SBI	SBV	NSB
	Serrate			Toothed	Smooth —absent			
	FT	CT						
Siphanoptera			+	+			+	
Nannochoristidae			+		+			+
Tipulidae			+		+			+
Nymphomyiidae			+		+			+
Deuterophlebiidae			+		+			+
Blephariceridae		+			+	+		
Axymyiidae			+		+			+
Pachyneuridae			+		+			+
Bibionidae			+		+			+
Mycetophilidae			+		+			+
Sciaridae			+		+			+
Cecidomyiidae			+		+			+
Psychodidae*			+		+			+
Psychodidae*	+			+			+	
Psychodidae*	+				+		+	
Trichoceridae			+		+			+
Perissommatidae			+		+			+
Anisopodidae			+		+			+
Scatopsidae			+		+			+
Synneuridae			+		+			+
Tanyderidae*	+				?	?		
Tanyderidae*			+		+			+
Ptychopteridae			+		+			+
Dixidae			+		+			+
Corethrellidae*			+		+			+
Corethrellidae*	+				+		+	
Chaoboridae			+		+			+
Culicidae*	+			+			+	
Culicidae*			+	+			+	
Culicidae*			+		+			+
Thaumaleidae			+		+			+
Simuliidae*	+			+			+	
Simuliidae*			+		+			+
Chironomidae*		+			+	?		
Chironomidae*			+		+			+

ments, third segment somewhat ovoid, with capitate sensilla not visible (fig. 2B), palp segment 3/4 + 5 = 1.38 (n = 1). **Thorax:** Anterior scutal apodemes not visible. Scutum pruinose, with a few scattered elongate setae, humeral pit of moderate size. Anapleural su-

ture elongate. Katepisternum with several setae. **Wing:** Length = 0.68–0.81 mm (n = 2), costal ratio = 0.33 (n = 1). Without macrotrichia, fine microtrichia present on all membrane. Alula without macrotrichia. Single radial cell present, radial veins compacted an-

TABLE 3
Relationship Between Feeding Habits of Families of Culicomorpha and Genera of Ceratopogonidae and Mouthpart Structure

FT = Finely toothed. CT = coarsely toothed. SBI = sucking blood from invertebrates. SBV = sucking blood from vertebrates. NSB = not sucking blood. More than one entry for a given genus is marked by an asterisk and indicates a variety of conditions present within that genus. ? = uncertain status.

Taxon	Mouthparts												
	Labrum		Mandible			Lacinia		Hypopharynx					
	Toothed	Smooth/ spi- cles	Serrate		Smooth	Toothed	Smooth	Toothed	Fine spi- cles	Smooth	SBI	SBV	NSB
			FT	CT									
Dixidae		+			+		+		+				+
Corethrellidae*		+	+				+	+				+	
Corethrellidae*		+			+		+		+				+
Chaoboridae		+			+		+		+				+
Culicidae*		+	+			+				+		+	
Culicidae*		+			+	+				+		+	
Thaumaleidae		+			+		+		+				+
Simuliidae*	+ ¹		+			+			+ ²			+	
Simuliidae*		+			+		+		+				+
Chironomidae*		+		+			+		+		?		
Chironomidae*		+			+		+		+				+
Leptoconops*		+	+			+			+			+	
Leptoconops*		+	+			+				+		+	
Austroconops		+	+			+		+				+	
Forcipomyia*		+			+		+		+				+
Forcipomyia*		+	+			+				+		+	
Forcipomyia*		+	+				+			+		+	
Forcipomyia*		+	+			bumps				+	+		
Forcipomyia*		+	+			ridges				+	+		
Forcipomyia*		+		+		prongs				+	+		
Forcipomyia*	+		+			+				+	?		
Atrichopogon*		+			+		+			+			+
Atrichopogon*		+		+		+				+	+		
Atrichopogon*		+	+			+			+		?		?
Atrichopogon*		+	+				+		+		?		?
Atrichopogon*		+	+				+			+			+ ³
Atrichopogon*		+	+				+	+			?		?
Dasyhelea		+			+		+			+			+
Culicoides*	+		+			+		+				+	
Culicoides*		+			+		+		+				+
Culicoides*		+		+		+			+		+		
Other Ceratopogoninae ⁴		+		+			+		+		+		
Other Ceratopogoninae*		+		+			+			+	+		
Other Ceratopogoninae*		+			+		+		+				+

¹ Thick, hooked teeth restricted to very apex.
² Spicules with thick bases.
³ Sucking contents of pollen.
⁴ Female adults of species of *Camptopterohelea* appear to have fine mandibular teeth but were not examined first-hand. Their biting habits are unknown.

teriorly. Base of M poorly defined, bifurcation not visible, both M₁ and M₂ present. **Legs** (fig. 2C–E): Femora, tibiae moderately robust. Legs with row of thick spines on first

and fifth tarsomere of each leg, hind first tarsomere with 3 or 4 rows of thick setae. Pair of thick setae on fore- and midleg trochanter absent. Midleg tibia with apical spur. Hind

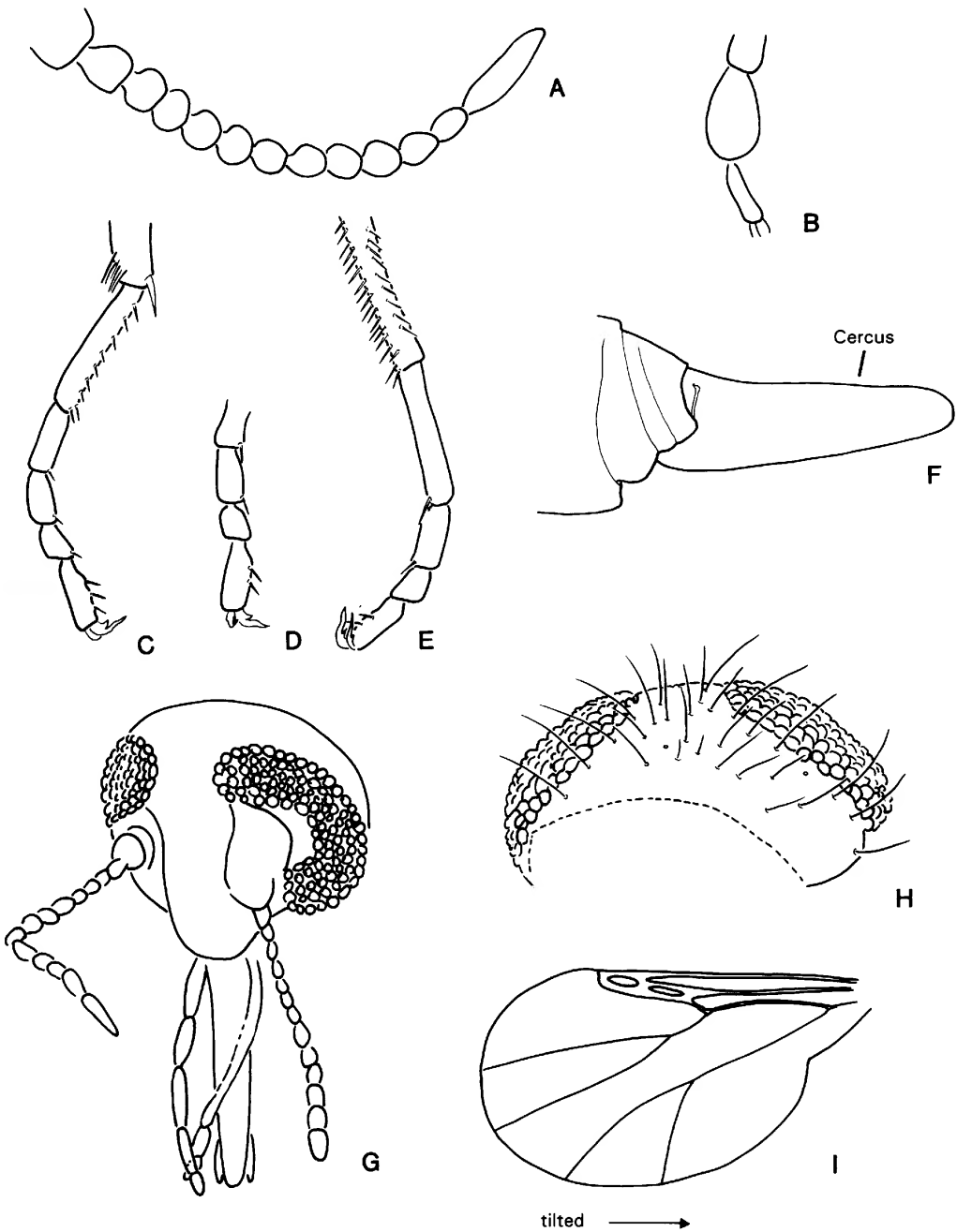


Fig. 2. A–F. Structures of female *Leptoconops curvachelus* (all of holotype). G–I. Structures of female *Alautunmyia elongata* (all of holotype). A. Antenna. B. Palp. C. Foreleg. D. Midleg. E. Hindleg. F. Lateral view of genitalia. G. Oblique anterolateral view of head. H. Posterodorsal view of head capsule. I. Wing.

first tarsomere without thick basal spine, without palisade setae. Foreleg, midleg, hindleg claws equal, with subapical bend, with thick inner tooth arising from near base of each talon (fig. 7D). Hindleg claw shorter than

fifth tarsomere. Claws of all legs of equal length, hind claw length/hind fifth tarsomere = 0.55 ($n = 1$). With short empodium. **Genitalia** (fig. 2F): Spermathecae not visible. Posterior margin of sternite 8 apparently lacking

thick setae. Details of sternite 9 not visible, apparently lacking lateral lobe bearing setae. Segment 10 not visible. Cercus elongate, laterally compressed, somewhat tapering apically.

DISTRIBUTION AND BIONOMICS: *L. curvachelus* is known from amber collected at Sunrise Landing Site, E. Brunswick and White Oaks Pits, Sayreville, New Jersey.

Based on the elongate cerci and the general habitat of extant members of the genus (as discussed above under *L. copiosus*), *L. curvachelus* likely bred in sandy, saline habitats.

The female paratype of *L. curvachelus* has a strikingly swollen abdomen (fig. 7C) and this may indicate that it is filled with either blood or nectar.

TAXONOMIC DISCUSSION: There is some question about the subgeneric placement of *L. curvachelus* because the placement of the capitate sensilla on palp segment 3 could not be determined. As such, *L. curvachelus* might belong to one of the following subgenera: *Holoconops* Kieffer, *Megaconops*, *Proleptoconops* or *Leptoconops* s. str. (i.e., those subgenera in which females have elongate cerci). I have placed it in *Leptoconops* s. str. because of the number of flagellomeres and the presence of a thick inner tooth on each claw, features currently considered diagnostic for this subgenus. However, these character states are not interpreted cladistically and are therefore suspect evidence for placement of the species.

The shape of the tarsal claws is distinctive among fossil *Leptoconops*. However, a number of extant species have similarly shaped claws with large basal teeth (e.g., *L. freeborni* Wirth (Wirth and Atchley, 1973); *L. melanderi* Wirth and Atchley (Wirth and Atchley, 1973); *L. bezzii* Noè (Clastrier and Coluzzi, 1973); *L. noei* Clastrier and Coluzzi (Clastrier and Coluzzi, 1973).

Both pieces of amber containing *L. curvachelus* are clear and free of contaminants. The holotype and paratype were in excellent condition and entirely opaque.

TYPES: Holotype, female adult in amber on microscope slide, labeled "Holotype *Leptoconops curvachelus* Borkent", "AMBER: Late Cretaceous, New Jersey: E. Brunswick, Sunrise Landing Site, G.R. Case, coll. AMNH no. NJ-45" (AMNH); paratype: 1 female in amber from White Oaks Pits, Sayreville,

Middlesex Co., New Jersey, AMNH NO. NJ-50A (AMNH).

DERIVATION OF SPECIFIC EPITHET: The name *curvachelus* (bent claw) refers to the subapical bend in the tarsal claws of females of this species.

KEY TO MALE FOSSIL *LEPTOCONOPS*

1. Apicolateral process moderately elongate, broad; inner margin of gonocoxite without elongate setae; outer margin of gonostylus with short seta 2
 ... *succineus* Szadziewski (Baltic amber, Eocene-Lower Oligocene)
- Apicolateral process very elongate, slender; inner margin of gonocoxite with elongate setae 2
2. Wing length 0.73–0.95 mm
 ... *primaevus* Borkent (Canadian amber, Upper Cretaceous)
- Wing length 0.57–0.62 mm
 ... *copiosus*, n. sp. (New Jersey amber, Upper Cretaceous)

KEY TO FEMALE FOSSIL *LEPTOCONOPS*

1. Tarsal claws evenly curved from base, with or without very slender inner tooth 2
 – Tarsal claws with subapical bend, with large inner tooth
 ... *curvachelus*, n. sp. (New Jersey amber, Upper Cretaceous)
2. Antennal flagellomeres 7–11 oval
 ... *succineus* Szadziewski (Baltic amber, Eocene-Lower Oligocene)
- Antennal flagellomeres 7–11 squat or spherical 3
3. Antennal flagellomeres 7–11 squat
 ... *boreus* Kalugina (Taimyr amber, Upper Cretaceous)
- Antennal flagellomeres 7–11 spherical (fig. 1G)
 ... *primaevus* Borkent (Canadian amber, Upper Cretaceous)

Alautunmyia Borkent, new genus

TYPE SPECIES: *Alautunmyia elongata*, n. sp., the only included species.

DIAGNOSIS: *Male.* Unknown. *Female.* The only Ceratopogonidae with widely spaced ommatidia (frons lacking any transverse sutures) and a wing with both cells r_1 and r_{2+3} well-developed.

DESCRIPTION: *Female adult.* Head: Eyes bare. Ommatidia broadly separated dorso-medially, with single dorsomedial seta likely

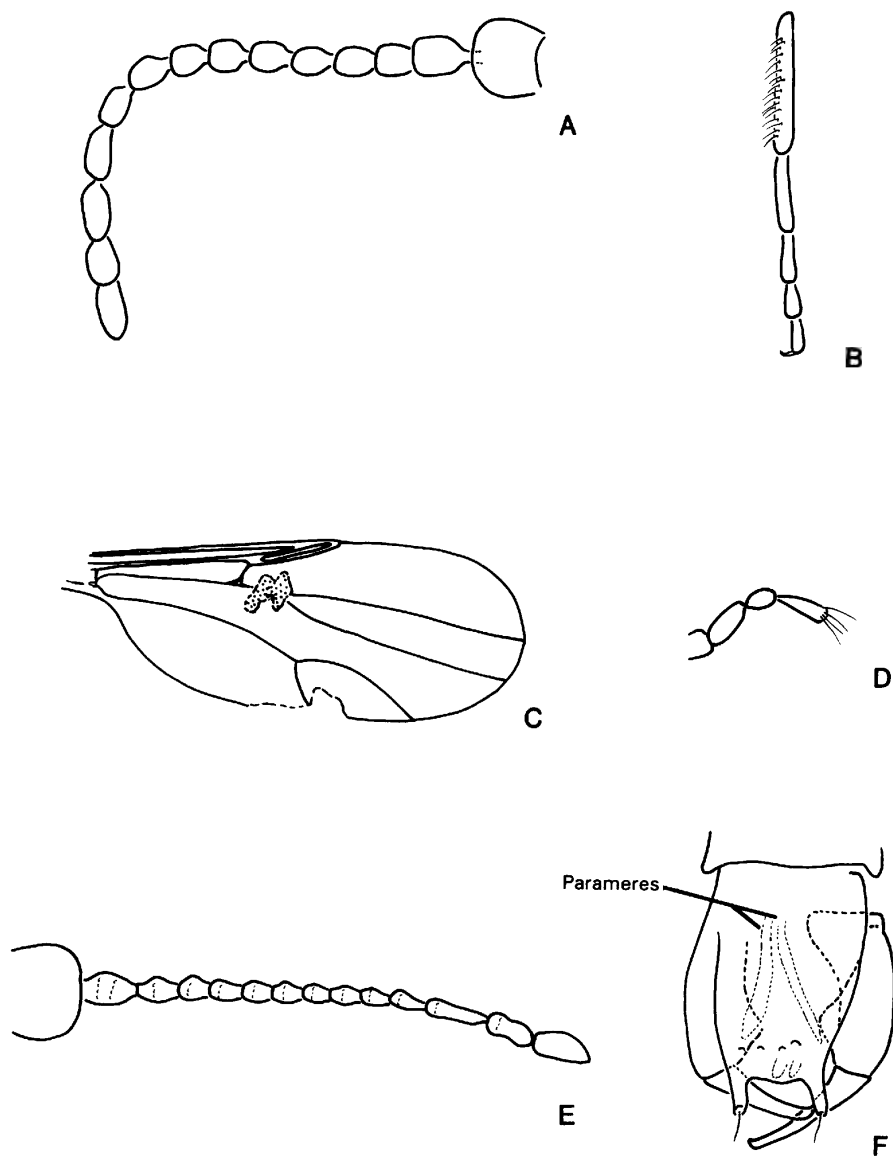


Fig. 3. A, B. Structures of female *Alautunmyia elongata* (all of holotype). C–F. Structures of male *Heleageron grimaldii* (all of holotype). A. Antenna. B. Hindleg. C. Wing. D. Palp. E. Antenna. F. Genitalia.

absent (fig. 2G, H). Antenna with 13 separate flagellomeres, sensilla on first flagellomere not visible (fig. 3A). Clypeus separated laterally by membrane from head capsule. Palp with five segments, capitate sensilla on third segment not visible (fig. 2G). **Thorax:** Anterior pronotal apodemes not visible. Scutum partially missing, with some scattered elongate setae, humeral pit not visible. Anapleural suture not visible. Katepisternal setae not vis-

ible. **Wing** (fig. 2I): Macrotrichia and microtrichia not visible. Alula not visible. Cells r_1 and r_{2+3} well-defined, short. M bifurcating distal to r-m. **Legs:** Femora, tibiae slender. Legs lacking armature, most details not visible. Hindleg first tarsomere without thick basal spine, without palisade setae but scattered stouter setae present (fig. 3B). Claws simple, inner tooth not visible, equal. Empodium not visible. Claws of all legs of equal

length. **Genitalia:** Details not visible except that cerci are short.

TAXONOMIC DISCUSSION: The structure of the head of *A. elongata* (fig. 2G) is similar to those of species of *Leptoconops*, exhibiting widely separated ommatidia. The wing (fig. 2I) is similar to those of extant *Culicoides*, *Ceratopogon*, and some other taxa of Ceratopogonini.

Remm (1976) described two species as having widely spaced ommatidia and a *Culicoides*-like wing: *Culicoides kaluginae* Remm and *Culicoides filipalpis* Remm. Borkent (1995) considered these reports of widely spaced ommatidia to be artifacts of observation due to awkward positioning of specimens in the amber (as was seen in a Canadian amber specimen which, when reoriented, proved to have closely approximated ommatidia). However, the discovery of *A. elongata* with this exact combination of features suggests that Remm's description may have been accurate and that both of his species may also belong in *Alautunmyia*. In particular, *C. filipalpis*, with its elongate mouthparts, looks very similar to *A. elongata*. Re-examination of the two Remm species is required to test for this possibility. If *C. filipalpis* is indeed a member of *Alautunmyia*, the specimens named *C. filipalpis* from Canadian amber by Borkent (1995: 53) will require a new name.

DERIVATION OF GENERIC EPITHET: The name *Alautunmyia* is based on the Mayan word "alautun" which denotes a 63 million year period and refers here to the Cretaceous age of this fly genus.

***Alautunmyia elongata* Borkent, new species**
Figures 2G-I, 3A-B

DIAGNOSIS: *Male.* Unknown. *Female.* As for the genus; this is the only included species.

DESCRIPTION: *Female adult.* Head: Antennal ratio = 0.71, terminal flagellomeres increasingly longer than more basal flagellomeres (fig. 3A). Mouthparts moderately elongate (fig. 2G), details of mouthpart structure not visible. Palp markedly elongate with segment 4, 5 short (fig. 2G), palp segment 3/4 = 2.00. **Wing** (fig. 2I): Length = 0.54 mm, costal ratio = 0.62. **Genitalia:** Details not visible.

DISTRIBUTION AND BIONOMICS: *Alautunmyia elongata* is known from amber collected at White Oaks Pit, Sayreville, New Jersey.

Included among contaminants in the amber holding the holotype are a number of trichomes that are similar to those of *Quercus*. Although these may indicate the period of leafing out (Borkent and Grogan, 1995), their presence in a different plane of resin flow means that they cannot be used to indicate possible early seasonality for *Alautunmyia elongata*. Trichomes have not been previously recorded from New Jersey amber.

TAXONOMIC DISCUSSION: The holotype of *A. elongata* is in rather poor condition. It appears to be partially decomposed and some of the cuticle is fragmented. Furthermore, the amber in which it is embedded contains contaminants (including many very small spheroids), reducing the visibility of the fossil. Finally, there appears to be a milky, translucent material covering some of the ventrum of the body, making especially the apex of the abdomen irritatingly difficult to see.

During preparation, the piece of amber in which the holotype is found split in two along the plane of the wings. As a result, the wings are mounted under a separate coverslip (on the same slide as the holotype).

TYPES: Holotype, female adult in amber on microscope slide, labeled "Holotype *Alautunmyia elongata* Borkent", "AMBER: Late Cretaceous, New Jersey: Middlesex Co., Sayreville, White Oaks Pit, Aug. 1992, Gerard R. Case, coll, AMNH no. NJ-47" (AMNH).

DERIVATION OF SPECIFIC EPITHET: The name *elongata* refers to the long mouthparts of the female adult.

***Atriculicoides globosus* (Boesel)**
Figure 8A

Lasiohelea globosa Boesel, 1937: 47. Cedar Lake, Manitoba. Upper Cretaceous.

Atriculicoides globosus: Borkent, 1995: 39.

Lasiohelea cretea Boesel, 1937: 46. Cedar Lake, Manitoba. Upper Cretaceous.

DIAGNOSIS: *Male and female:* The only species of *Atriculicoides* with palpal segment 3 without a pit and with thick spines on the first tarsomere of the foreleg.

DISTRIBUTION AND BIONOMICS: *Atriculicoides globosus* was previously known only

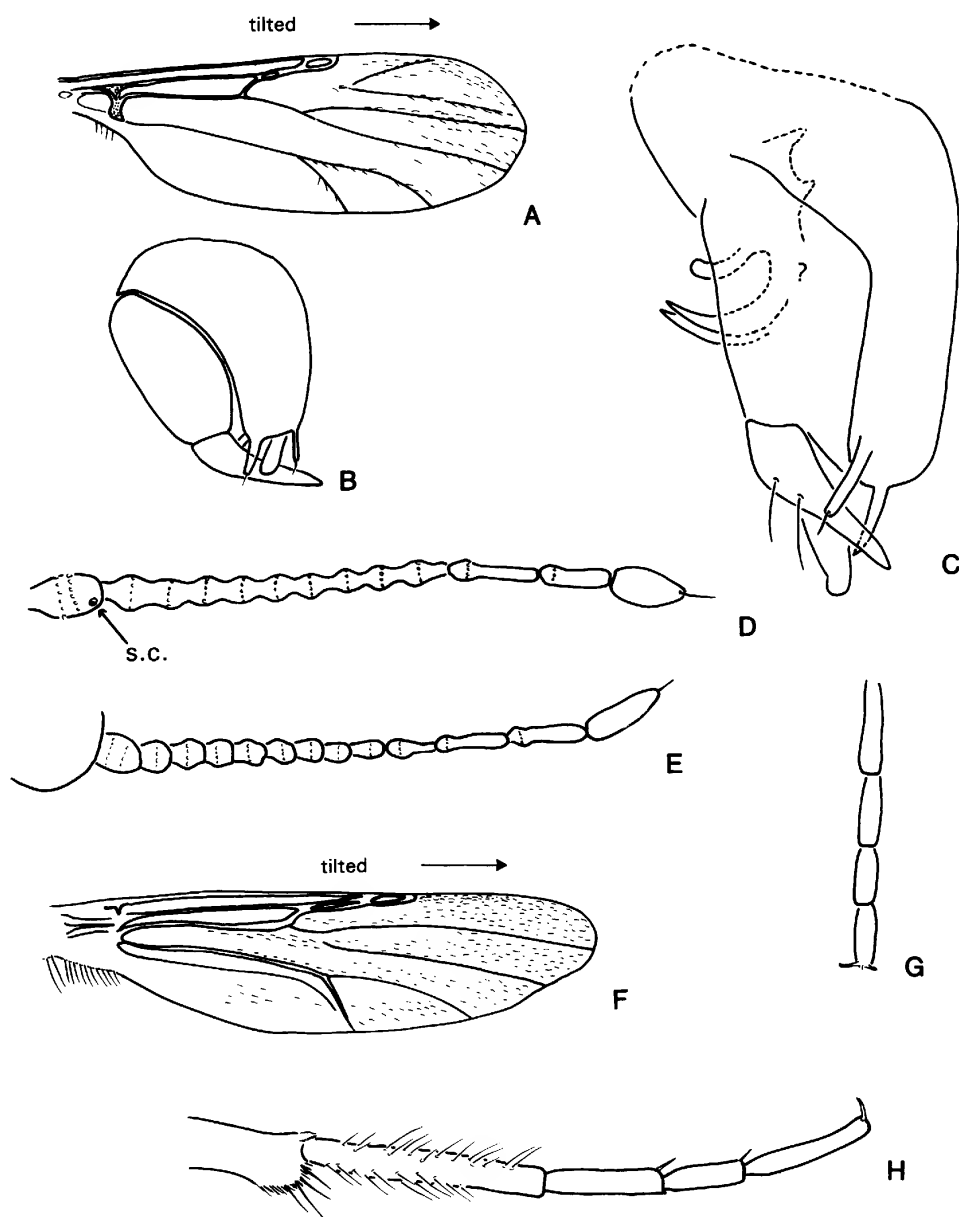


Fig. 4. A–D. Structures of male *Culicoides casei*. E–H. Structures of male *Culicoides bifidus* (all of holotype). A. Wing (NJ-51A). B. Genitalia (NJ-51A). C. Genitalia (NJ-43). D. Antenna (NJ-43). E. Antenna. F. Wing. G. Foreleg. H. Hindleg.

from Canadian amber (Borkent, 1995). Based on observations of the mouthparts of females from Canadian amber (finely toothed mandibles), it is probable that this species fed on vertebrate blood (see further discussion below under *C. grandibocus*).

The piece of amber containing *A. globosus* also included a male Tanypodinae (Chiro-

nomidae) and an unidentified female chironomid.

TAXONOMIC DISCUSSION: All visible attributes of the single New Jersey amber female are consistent with those of *A. globosus* from Canadian amber. The specimen (fig. 8A) was in moderately good condition (body tissues partly decomposed, cuticle undistorted) and

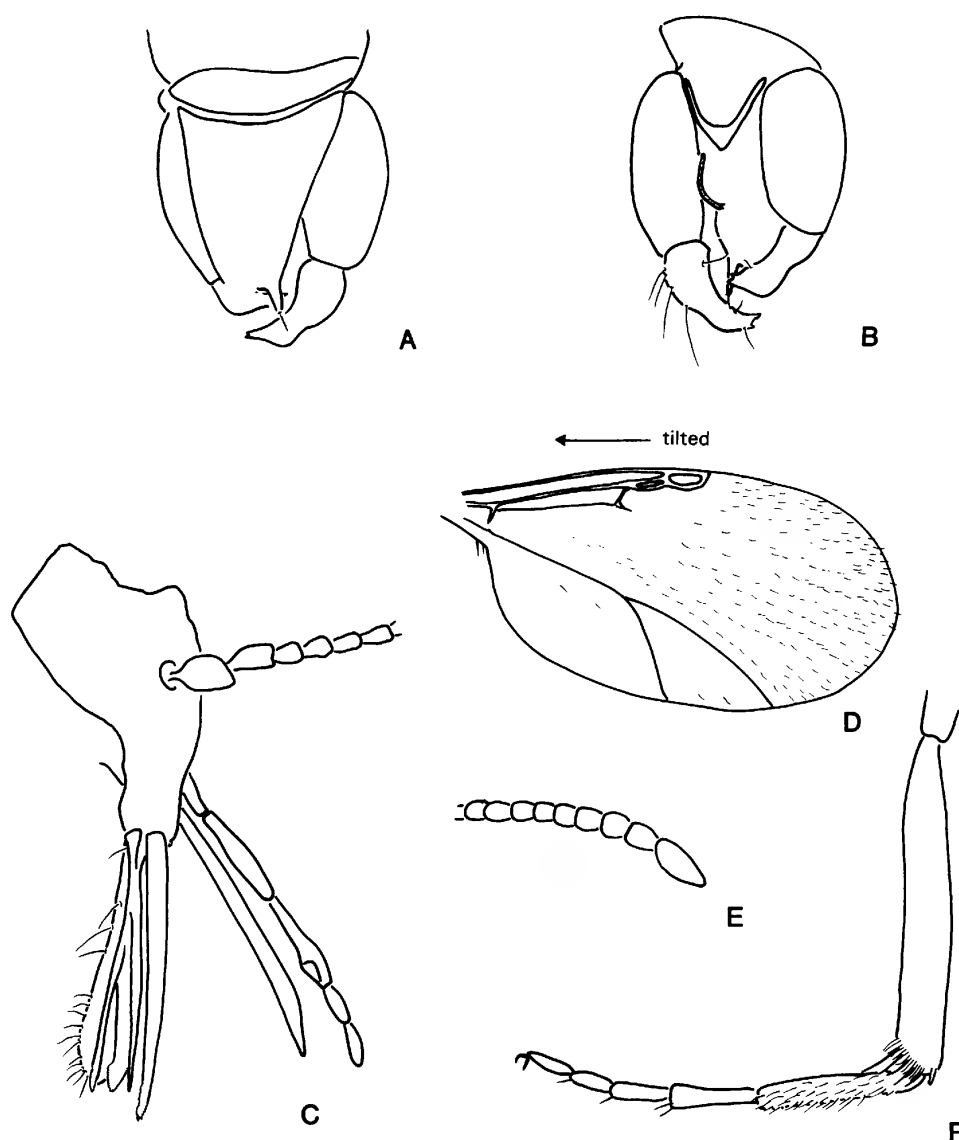


Fig. 5. A, B. Male genitalia of *Culicoides bifidus* (all of holotype). A. Dorsolateral view of genitalia. B. Ventrolateral view of genitalia. C–F. Structures of *Culicoides grandibocus* (all of holotype). C. Lateral view of head capsule. D. Wing. E. Terminal flagellomeres of antenna. F. Hindleg.

details of the wing, legs (especially the presence of thick spines on the first tarsomere of the foreleg), and mouthparts (especially palp segment 3) all fit the description given by Borkent (1995). The only difference found was that the wing length was slightly shorter in the New Jersey specimen (0.89 mm) than those in Canadian amber (0.92–1.26 mm, $n = 17$).

MATERIAL EXAMINED: 1 female from New Jersey amber (AMNH No. NJ-90C). From

Canadian amber: 13 males, 30 females from Canadian amber [as reported by Borkent, 1995].

***Heleageron grimaldii* Borkent,**
new species
Figures 3D–F, 8B

DIAGNOSIS: *Male*. The only species of *Heleageron* with a gonostylus tapering gradually to a slightly curved apex. *Female*. Unknown.

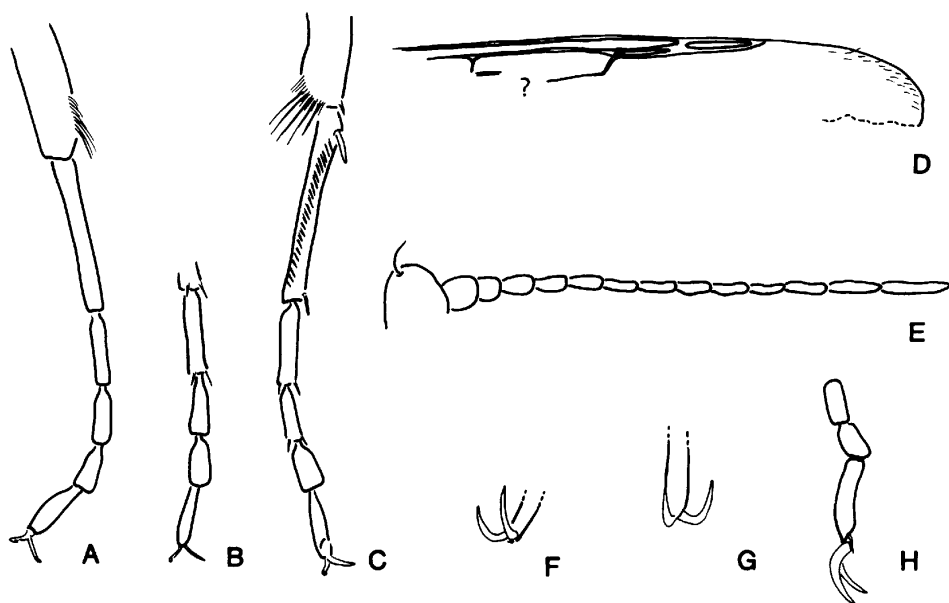


Fig. 6. A–C. Structures of male *Palaeobrachypogon remmi* (NJ-46). D–H. Structures of female *Palaeobrachypogon remmi* (NJ-92). A. Foreleg. B. Midleg. C. Hindleg. D. Anterior portion of wing. E. Antenna. F. Claws of midleg. G. Claws of hindleg. H. Tarsomeres 3–5 of hindleg.

DESCRIPTION: Male adult. Head: Eyes bare, separation dorsomedially uncertain. Dorsomedial seta on vertex not visible. Antenna with well-developed plume, basal foramen of pedicel not visible, 13 separate flagellomeres, antennal ratio = 0.48, flagellomere 10/11 = 0.57, 10–13 more elongate than preceding flagellomeres (fig. 3E), first flagellomere sensilla coeloconica not visible. Mouthparts moderately elongate, mouthpart length/length of fifth tarsomere of foreleg = 4.12. Palp with five segments, third segment short, cylindrical, with capitate sensilla not visible, palp segment 3/4 = 1.25 (fig. 3D). **Thorax:** Anterior scutal apodemes not visible. Scutum bare of pruinosity, with scattered elongate setae, humeral pit not visible. Anapleural suture not visible. Katepisternal setae not visible. **Wing** (fig. 3C): Length = 0.52 mm, costal ratio = 0.55. Without macrotrichia, fine microtrichia present on all membrane. Alula without macrotrichia. Single radial cell well-defined. M bifurcating distal to r-m. **Legs:** Femora, tibiae slender. Legs lacking armature except for apex of most tarsomeres (not all visible) with pair of thick setae. Fore- and midleg trochanter each with pair of thick setae. Midleg tibia without apical spur. Hindleg

first tarsomere without thick basal spine, without palisade setae. Apex of claws not clearly visible but appearing simple. Without empodium. **Genitalia** (fig. 3F, 8B): Apicolateral process elongate, thick, with apical seta. Gonocoxite somewhat short, thick. Gonostylus thick basally, tapering to slightly hooked apex. Paramere slender, elongate apically. Aedeagus not visible, but if present, small, basal.

DISTRIBUTION: *Heleageron grimaldii* is only known from amber collected at White Oaks Pit, Sayreville, New Jersey.

TAXONOMIC DISCUSSION: *Heleageron grimaldii* is similar to the only other member of the genus, *H. arenatus*. Differences in the shape of the gonostylus and the relative length of the terminal flagellomere indicate, however, that the two are distinct.

Borkent (1995) noted that the presence of elongate setae on the hind tibia was a feature of the genus *Heleageron*. This feature was difficult to confidently access for *H. grimaldii* because some setae were broken from the body surface, including the left hind tibia (presumably by resin flow) and the right hind tibia was broken when the amber was split. Nevertheless, some elongate setae were pres-

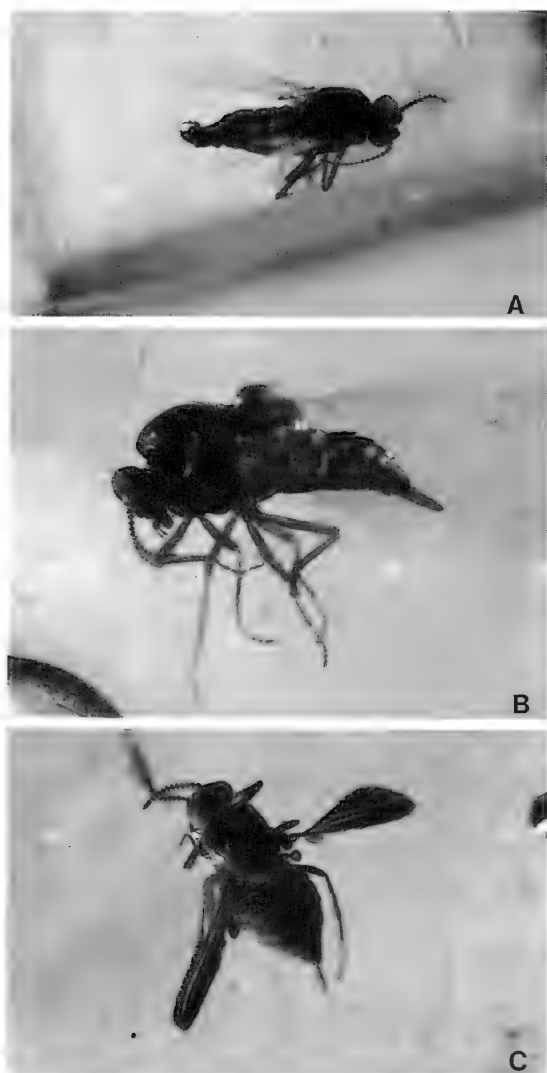


Fig. 7. A. Habitus of male *Leptoconops copiosus* (NJ-41A). B. Habitus of female *Leptoconops curvachelus* (holotype). C. Habitus of female *Leptoconops curvachelus* (NJ-50A).

ent near the right hind tibia which likely originated from that structure.

The holotype of *H. grimaldii* is in a rather opaque, yellowish-white piece of amber containing a dense cloud of bubbles. Fortunately, the piece could be split in half along a plane containing the specimen so that details could be seen. The amber containing the fossil was cylindrical before grinding and polishing.

TYPES: Holotype, male adult in amber on microscope slide, labeled "Holotype *Heleageron grimaldii* Borkent", "AMBER: Late

Cretaceous, NEW JERSEY: Middlesex Co. Sayreville, White Oaks Pits, Aug.,-Nov. 1994, coll. AMNH no. NJ-91" (AMNH).

DERIVATION OF SPECIFIC EPITHET: The name *grimaldii* is proposed in thanks to David Grimaldi who has built a wonderful collection of New Jersey amber at the AMNH and so heartily supported the study of the material reported on in this paper.

Culicoides casei

Grogan and Szadziewski

Figures 4A-D

Culicoides? casei Grogan and Szadziewski, 1988: 809. Sayreville, New Jersey. Upper Cretaceous. *Culicoides casei*: Borkent, 1995: 66.

DIAGNOSIS: *Male.* The only Cretaceous species of *Culicoides* with macrotrichia restricted to area distal to fork of M and Cu and gonostylus undivided, with swollen base and apical portion more or less straight. *Female.* Unknown.

The following description is supplemental to that given by Borkent (1995). Only modified character states are given here.

DESCRIPTION: *Male adult.* **Head:** Antenna with flagellomeres 2-10 fused, antennal ratio = 0.53-0.65, flagellomere 10/11 = 0.53-0.60, first flagellomere with sensilla coeloconica (fig. 4D). Mouthpart length/length of fifth tarsomere of foreleg = 2.23-3.00. **Wing** (fig. 4A): Length = 0.59-0.80, costal ratio = 0.54-0.62. Macrotrichia present on apical half of wing distal to fork of M, some on membrane but others concentrated along wing veins. Alula with macrotrichia. **Legs:** At least midleg trochanter with pair of thick setae. Hindleg tibia with apical spur. **Genitalia** (fig. 4B, C): Apicolateral process elongate, slender, with apical seta. Gonocoxite somewhat short, thick. Gonostylus thick basally, tapering gradually to pointed apex. Parameres separate, each with subbasal ventral projection, curved, elongate apically. Aedeagus forming single median structure with short extension tapering posteriorly, shape of apex uncertain.

DISTRIBUTION AND BIONOMICS: *Culicoides casei* is now known from three males in amber, all collected at Sayreville, Middlesex Co., New Jersey.

TAXONOMIC DISCUSSION: The two additional males reported in this study were iden-



Fig. 8. A. Habitus of female *Atriculicoides globosus* (NJ-90C). B. Habitus of *Heleageron grimaldii* (holotype). C. Habitus of male *Culicoides bifidus* (holotype).

tified as *C. casei* because they were similar to the holotype (including their genitalia). Both specimens, however, were somewhat smaller than the holotype although well within the range of variation known for extant species of *Culicoides*.

Borkent (1995) noted that there was some question about the report of a weak row of palisade setae by Grogan and Szadziewski (1988). The presence of only scattered setae on the first tarsomere of the hindleg of the two additional specimens confirms that this state was originally misinterpreted by Grogan and Szadziewski (1988).

The short, pointed apex of the gonostylus

drawn for *C. casei* by Borkent (1995) is due to the angle of observation. In fact, the apex is stouter and proportionally longer than shown; it is similar to that shown for the specimens reported here (fig. 4B, C).

One of the two additional specimens was in good condition (NJ-51A) but the other was in poor shape (NJ-43). Both pieces of amber included some spherical contaminants (at least some of these are gas bubbles), obscuring some details.

MATERIAL EXAMINED: 3 males: holotype (PMNH) and 2 males (AMNH no. 43, AMNH no. 51A).

DERIVATION OF SPECIFIC EPITHET: The name

casei refers to the collector of the holotype, Gerard R. Case, who also collected a number of the specimens described here.

***Culicoides bifidus* Borkent, new species**

Figures 4E–H, 5A,B, 8C

DIAGNOSIS: *Male*. The only Cretaceous species of *Culicoides* with macrotrichia scattered on wing membrane (including cells cua_1 and cua_2) and the gonostylus apically bifid near the very apex. *Female*. Unknown.

DESCRIPTION: *Male adult*. **Head:** Eyes bare, narrowly separated dorsomedially. Vertex with single dorsomedial seta. Antenna with well-developed plume, basal foramen of pedicel not visible, 13 separate flagellomeres, antennal ratio = 0.68, flagellomere 10/11 = 0.62, flagellomeres 10–13 more elongate than preceding flagellomeres (fig. 4E), first flagellomere sensilla coeloconica not visible. Mouthparts moderately elongate. Mouthpart length/length of fifth tarsomere of foreleg = 2.64. Palp with five segments, third segment short, cylindrical, with capitate sensilla not visible. **Thorax:** Anterior scutal apodemes not visible. Scutum pruinose, with scattered elongate setae, humeral pit well-developed. Anapleural suture short. Katepisternum without setae. **Wing** (fig. 4F): Length = 1.05 mm, costal ratio = 0.61. Macrotrichia scattered over most of wing, fine microtrichia on all membrane. Alula with macrotrichia. Cells r_1 and r_{2+3} well-defined, short. M bifurcating distal to r-m. **Legs** (fig. 4G, H): Femora, tibiae slender. Legs lacking armature. Fore- and midleg trochanter each with pair of thick setae. Midleg tibia without apical spur. Hindleg first tarsomere without thick basal spine, without palisade setae. Claws apically bifid. Without empodium. **Genitalia** (fig. 5A, B): Apicolateral process elongate, pointed, with apical seta. Gonocoxite short, thick. Gonostylus thick, outer margin indented at mid-length, tapering to bifid apex. Paramere slender, elongate apically. Aedeagus triangular, single median structure with short, tapering posterior extension.

DISTRIBUTION AND BIONOMICS: *Culicoides bifidus* is known from amber collected at Sunrise Landing Site, E. Brunswick, New Jersey.

The amber containing the holotype includes a part of an unidentified insect leg.

TAXONOMIC DISCUSSION: The male of *C. bifidus* is similar to *C. filipalpis* Remm (from Canadian and Taimyr amber) and *C. tyrrelli* (Boesel) (from Canadian amber) in having many macrotrichia on the wing and a divided gonostylus. However, the restriction of the division of the gonostylus to the very apex distinguishes *C. bifidus* from these other two Cretaceous species.

TYPES: Holotype, male adult in amber on microscope slide, labeled "Holotype *Culicoides bifidus* Borkent", "NEW JERSEY amber: Late Cretaceous, AMNH no. NJ-93, Diptera: ♂ ceratopogonid, Sunrise Landing site, E. Brunswick (Middlesex Co.)" (AMNH)

DERIVATION OF SPECIFIC EPITHET: The name *bifidus* refers to the shape of the apex of the gonostylus.

***Culicoides grandibocus* Borkent,**

new species

Figures 5C–F

Diagnosis: *Male*. Unknown. *Female*. The only Cretaceous species with a markedly elongate palp in which segments 2 and 3 are long, slender, and cylindrical and with a wing with most macrotrichia restricted to the distal half.

DESCRIPTION: *Female adult*. **Head:** Eyes bare, dorsomedial separation, vertex not visible. Antenna with 13 separate flagellomeres, flagellomere 13 more elongate than preceding flagellomeres (fig. 5E), antennal ratio not measurable, sensilla coeloconica on first flagellomere not visible. Mouthparts markedly elongate (fig. 5C), mouthpart length/length of fifth tarsomere of foreleg = 5.00. Separation of clypeus from head capsule not visible. Labrum with large teeth. Mandible with fine teeth (approximately 16 present). Lacinia with fine teeth, details not visible. Hypopharynx not visible. Palp with five segments, second and third markedly elongate, nearly cylindrical, third with capitate sensilla arranged in pit, palp segment 3/4 = 2.47. **Thorax:** Details not visible. **Wing** (fig. 5D): Length = 0.53 mm, costal ratio = 0.51. Macrotrichia more or less restricted to distal half of wing, microtrichia present on all membrane. Alula with macrotrichia. Cells r_1 and r_{2+3} well defined, short. Bifurcation of M not visible. **Legs:** Femora, tibiae slender. Legs lacking

armature, except for apex of all tarsomeres with pair of apical thick setae (fig. 5F). Pair of thick pair of setae on fore- and midleg trochanter not visible. Midleg tibia without apical spur. Hindleg first tarsomere without thick basal spine, without palisade setae (fig. 5F). Foreleg, midleg, hindleg claws equal, simple, with fine inner teeth, without empodia. Hindleg claw shorter than fifth tarsomere (fig. 5F). **Genitalia:** Details not visible other than cerci of moderate length.

DISTRIBUTION AND BIONOMICS: *C. grandibocus* is known from amber collected at Sayreville, Middlesex Co., New Jersey.

Borkent (1995) discussed in detail the correlation between various mouthpart modifications and different feeding modes. Tables 15 and 16 in Borkent (1995) provided the basis for the interpretation of feeding mode in relation to the structure of ceratopogonid mouthparts but were misprinted. The tables are presented here again (as tables 2 and 3) in their correct form. The presence of both a finely toothed mandible and a lacinia with teeth is found only in extant species that suck blood from vertebrates. Furthermore, most species of extant *Culicoides* that have an elongate, slender third maxillary palp segment feed on large mammals (likely correlated with few capitate sensilla, structures that detect CO₂ concentrations emanating from the host). The presence of all these features in *C. grandibocus* suggests that the female likely fed on large dinosaurs, the only large vertebrates around during the Late Cretaceous.

The amber containing the holotype of *C. grandibocus* also included a Baetidae mayfly, indicating the presence of nearby aquatic habitat (extant Baetidae occur in both lotic and lentic habitats).

TAXONOMIC DISCUSSION: This species is similar to the younger *C. filipalpis* Remm, which is known from Canadian (Campanian) and Taimyr (Coniacian-Santonian) amber; both species are the only fossil species of *Culicoides* that have strikingly elongate mouthparts. *Culicoides grandibocus* differs from *C. filipalpis* in having fewer macrotrichia on the wing, a well-defined pit on the third maxillary segment, and flagellomeres 1–12 more or less of equal length (although this last feature may be an artifact produced by distortion of the specimen).

The other two species of *Culicoides* recorded from New Jersey amber are known only from male specimens and there is the possibility that *C. grandibocus*, known only from a female, is conspecific with either one of these. However, significant differences suggest that *C. grandibocus* is indeed a validly recognized species. *Culicoides casei* males have short mouthparts, while the female of *C. grandibocus* has very long ones. Males and females of the closely related *C. filipalpis* are probably correctly associated and both have elongate mouthparts. Furthermore, in most instances where the females of extant species of ceratopogonids have elongate mouthparts, the males do also, suggesting that the male of *C. grandibocus*, when discovered, will have the same feature. The male of *C. bifidus* has more macrotrichia on the wing (fig. 4F) than does the female of *C. grandibocus* (fig. 5D), indicating that they are probably not conspecific. Extant species of Ceratopogonidae males always have fewer macrotrichia than females.

The holotype of *C. grandibocus* was in a partially deteriorated state, with the head capsule, thorax, and abdomen badly deformed. The antennae were at least somewhat distorted. If further material becomes available for study, the characterization of these features here should be checked.

TYPES: Holotype, female adult in amber on microscope slide, labeled "Holotype *Culicoides grandibocus* Borkent", "AMBER: Late Cretaceous, NEW JERSEY: Middlesex Co. Sayreville, White Oaks Pit, Aug.-Nov., 1993, coll. AMNH no. NJ-15B" (AMNH).

DERIVATION OF SPECIFIC EPITHET: The name *grandibocus* (large, mouth) refers to the very long mouthparts of this species.

KEY TO CRETACEOUS *CULICOIDES*

The following key is modified from Borkent (1995) to incorporate newly discovered character states in the additional specimens of *C. casei* reported on above and *C. bifidus*, n. sp. Only males are keyed because the females of *C. casei* and *C. bifidus* are unknown.

Culicoides grandibocus, known only as a female, will key to *C. filipalpis* in Borkent (1995) but may be distinguished by the presence of fewer macrotrichia on the wing and

the presence of a well-defined maxillary palp pit. The female of *C. filipalpis* has macrotrichia over the entire wing surface and has no pit on the third maxillary palp segment.

1. Gonostylus divided apically or with inner, subapical lobe (fig. 5A, B) 2
- Gonostylus tapering to pointed apex (fig. 4B, C) 4
2. Gonostylus with tricusate apex *filipalpis* Remm
(Canadian and Taimyr amber, Upper Cretaceous)
- Gonostylus with inner subapical lobe or appearing to have bifurcate apex 3
3. Gonostylus with inner subapical lobe or appearing to have deeply bifurcate apex *tyrrelli* (Boesel)
(Canadian amber, Upper Cretaceous)
- Gonostylus bifurcate at very apex (fig. 5A, B) *bifidus*, n. sp.
(New Jersey amber, Upper Cretaceous)
4. Gonostylus with a thick base, gradually tapering to apex 5
- Gonostylus slender, of nearly even diameter for most of length 10
5. Wing with macrotrichia restricted to area distal to fork of M and Cu (fig. 4A) 6
- Wing with macrotrichia present basal of fork of M and Cu (fig. 4F) 9
6. Apicolateral process gradually tapering to pointed apex *sphenostylus* Remm
(Taimyr amber, Upper Cretaceous)
- Apicolateral process cylindrical for most of its length, tapering only near very apex (fig. 4B, C) 7
7. Gonostylus chelate, with mediobasal lobe *obuncus* Borkent
(Canadian amber, Upper Cretaceous)
- Gonostylus gradually tapering from thick base (fig. 4B, C) 8
8. Outer margin of gonostylus evenly curved *annosus* Borkent
(Canadian amber, Upper Cretaceous)
- Apical portion of gonostylus more or less straight (fig. 4B, C) *casei* Grogan and Szadziewski
(New Jersey amber, Upper Cretaceous)
9. Apicolateral process thick, broad, tapering near apex *canadensis* (Boesel)
(Canadian amber, Upper Cretaceous)
- Apicolateral process tapering gradually to narrow apex *agamus* Borkent
(Canadian amber, Upper Cretaceous)
10. Apicolateral processes of moderate size, tapering to apex; gonostylus very slender for entire

- length *succineus* Remm
(Taimyr amber, Upper Cretaceous)
- Apicolateral processes very small, knoblike; gonostylus thick for entire length *bullus* Borkent
(Canadian amber, Upper Cretaceous)

***Palaeobrachypogon remmi* Borkent**
Figures 6A–H

Palaeobrachypogon remmi Borkent, 1995: 76. 5 km S. Grassy Lake, Alberta. Upper Cretaceous.

DIAGNOSIS: *Male*. The only Cretaceous species of Ceratopogonidae in New Jersey amber with the hindleg first tarsomere bearing a strong basal spine and with a well-developed row of palisade setae. *Female*. The only Cretaceous species of Ceratopogonidae with macrotrichia restricted to apical margin of the wing membrane, with well-developed moderately elongate radial cells, with a strong basal spine and row of palisade setae on the first tarsomere of the hindleg, with the hindleg claw elongate (hindleg claw/fifth tarsomere > 0.8) and with the fore, mid and hindleg claws more or less equal in size and with inner teeth.

DESCRIPTION (includes only those features evident in the New Jersey amber fossils): *Male adult*. **Head:** Antenna with well-developed plume, 13 flagellomeres, 11–13 appearing more elongate than preceding flagellomeres, flagellomere 13 tapering to apex. **Legs** (fig. 6A–C): Femora, tibiae somewhat thick. Hindleg tibia with spur. Hindleg first tarsomere with thick basal spine, with row of palisade setae extending entire length. Claws apically bifid.

Female adult. **Head:** Eyes bare, narrowly separated dorsomedially. Vertex with single dorsomedial seta present. Antenna (fig. 6E) with 13 separate flagellomeres, 9–13 more elongate than preceding ones, sensilla coeloconica on first flagellomere not visible. Mouthparts moderately elongate, details not visible. Membrane separating clypeus from head capsule not visible. Palpus with five segments, further details not visible. **Thorax:** Anterior scutal apodemes not visible. Scutum pruinose, with scattered elongate setae, humeral pit not visible. Anapleural suture not visible. Katepisternal setae not visible.

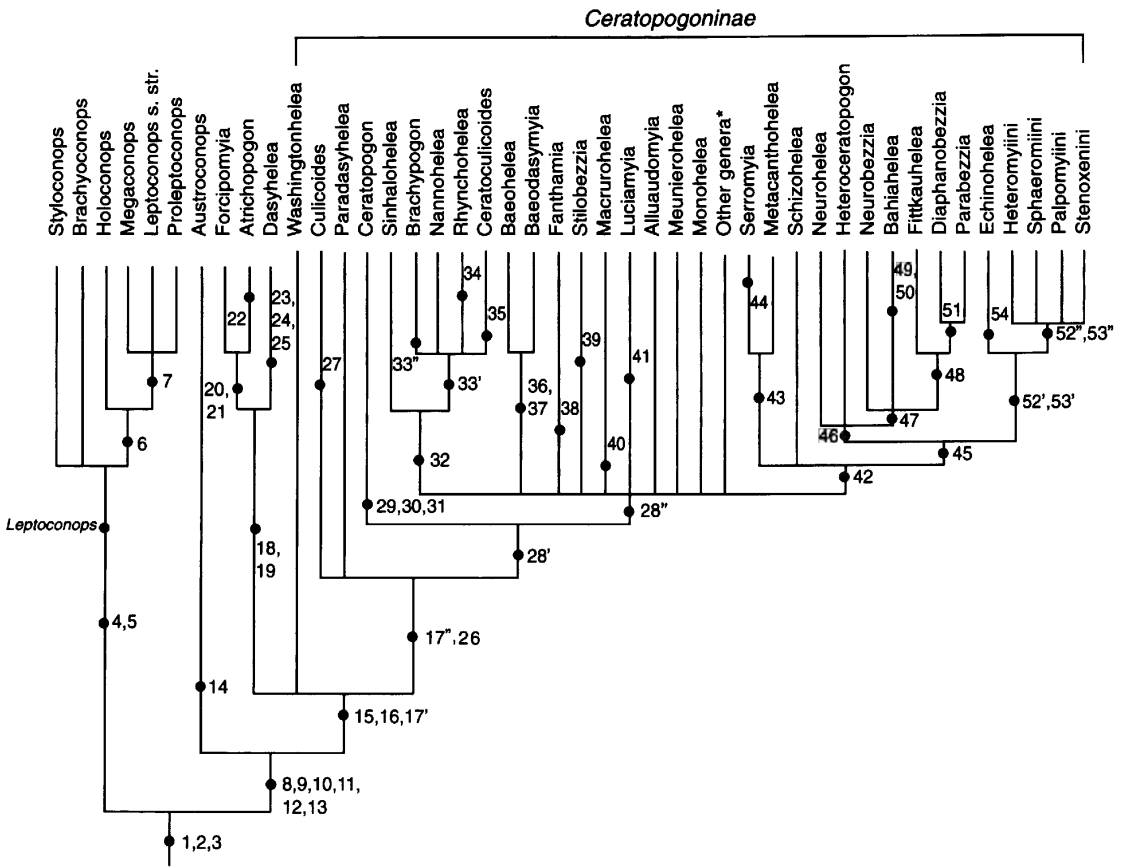


Fig. 9. Cladistic relationships of extant lineages of Ceratopogonidae (from Borkent, 1995). Numbers refer to synapomorphies listed in table 1.

* Represents unresolved lineages described as the following genera. Each arises as a single lineage from the group delineated by synapomorphies 28'' and 42: *Afrohelea*, *Allohelea*, *Alluaudomyia*, *Ankylohelea*, *Austrohelea*, *Boreohelea*, *Borkenthelea*, *Bothahelea*, *Bothamia*, *Cacaohelea*, *Calcarhelea*, *Camptopterohelea*, *Capehelea*, *Ceratohelea*, *Chelohelea*, *Congohelea*, *Downeshelea*, *Heterohelea*, *Kolenhelea*, *Monohelea*, *Neohelea*, *Notiohelea*, *Notoceratopogon*, *Paralluaudomyia*, *Parastilobezzia*, *Pseudostilobezzia*, *Schizonyxhelea*, *Stiloculicoides*.

Wing (fig. 6D): Macrotrichia present along apical margin of wing membrane, very fine microtrichia present on all membrane. Macrotrichia on alula not visible. Radial cells well-developed. Bifurcation of M not visible. **Legs**: Femora, tibiae somewhat thick. Legs lacking armature, except apex of each tarsomere of each leg with pair of thick setae. Pair of thick setae on fore- and midleg trochanter not visible. Midleg tibia without apical spur. Hindleg first tarsomere with thick basal spine, with palisade setae along entire length. Foreleg, midleg, hindleg claws equal, simple, inner tooth not visible, claws from each leg of about equal length (fig. 6F–H, 8D).

Hindleg claw shorter than fifth tarsomere. Without empodium. **Genitalia**: Most details not visible. Cerci of moderate length.

DISTRIBUTION AND BIONOMICS: *Palaeobrachypogon remmi* is known from Canadian amber (1 male, 3 females) and from White Oaks Pit, Sayreville, New Jersey.

These New Jersey amber specimens represent the oldest known members of the lineage of what is generally considered to be insectivorous Ceratopogoninae (defined by character 28', fig. 9). Palisade setae are only present on insectivorous Ceratopogonidae that feed on insects of equal or smaller size, generally other swarming Nematocera (with

the exception of some derived *Palpomyia* that feed on large Ephemeroptera). The presence of a species with palisade setae in New Jersey amber therefore suggests that some Ceratopogonidae have been preying on other Nematocera for at least 88–93.5 million years.

The amber containing the female of *P. remmi* also included a single leg of an unidentified Diptera (probably a chironomid).

TAXONOMIC DISCUSSION: The male specimen was in very poor condition and therefore only a few of its features could be recorded here. Aside from being badly deteriorated, most of the dorsum of the head and thorax (including wings) are missing. Most structures were so distorted as to be uninterpretable (including the genitalia). Finally, the amber piece containing the specimen includes some gas bubbles. The female specimen was also partially decomposed but its cuticle was in reasonable condition. Furthermore, a globular mass obscured some details of the legs.

The association of the male and female is rather tenuous, considering the terrible condition of the male and the moderate state of the female. They were considered conspecific on the basis of the shared similarity of the hindleg first tarsomere (bearing palisade setae and a strong basal spine) and the fact that they represented the only Ceratopogonini in New Jersey amber.

Although the two specimens were identified as *P. remmi*, there were some small differences between the New Jersey female and those from Canadian amber. In the New Jersey female the wing length was shorter (0.65 mm, compared to 0.87–0.98 in Canadian amber) and no inner teeth were visible on the claws (perhaps due to preservation and angle of observation). Future specimens may indicate that the New Jersey material represents another species of *Palaeobrachypogon*.

MATERIAL EXAMINED: From New Jersey amber: 1 male (AMNH no. NJ-46), 1 female (AMNH no. NJ-92). From Canadian amber: 1 male, 3 females [as reported by Borkent, 1995].

PHYLOGENETIC INTERPRETATION

The following analysis is taken from that given for Canadian Cretaceous amber Ceratopogonidae by Borkent (1995) and is based

on an analysis of the cladistic relationships of extant lineages. Numbers for synapomorphies correspond to those given in that work (fig. 9). The characters and their states are merely listed here (table 1) and outgroup comparisons justifying polarity decisions are provided by Borkent (1995).

Each of the fossils from New Jersey amber is presented below in its own cladogram. Numbers indicate only those character states which could be recorded for the fossil, allowing the reader to gauge the reliability of the phylogenetic placement.

Leptoconops copiosus and *L. curvachelus*: Both these species are considered to be members of *Leptoconops* s. str., even though they might actually be more closely related to one of the other subgenera (see discussion under each species for specifics). Regardless, it is obvious that both are members of the genus (fig. 10A, B).

The recognition of two species of *Leptoconops* with elongate cerci (character 6) from the Turonian indicates that the genus must have diversified at an earlier date. Although neither *Styloconops* nor *Brachyconops* is known as a fossil, these must represent even earlier lineages if the phylogenetic interpretation here is correct (fig. 10A, B).

Alautunmyia: Available character states indicate that this genus forms one of the earliest lineages within the family (fig. 11A). Because of the poor condition of the single type specimen and the lack of an associated male, it is currently impossible to provide more specific cladistic analysis. *Alautunmyia* may be the sister group of the entire family, of *Leptoconops* or of all Ceratopogonidae other than *Leptoconops*.

The phylogenetic placement of *Alautunmyia* has implications for the interpretation of wing character states of some Ceratopogonidae. *Alautunmyia* has a wing with short but well-developed cells r_1 and r_{2+3} which taper both basally and apically (fig. 2I), similar to those of most *Culicoides* and some genera of Ceratopogonini (e.g., *Ceratopogon* Meigen, *Ceratohelea* Wirth and Grogan, some *Brachypogon* Kieffer). This suggests that this character state is plesiomorphic at or very near the base of the phylogeny of the Ceratopogonidae. As a consequence, the elongate radial cells that are nearly truncate basally and present in *Austroconops* Wirth and Lee

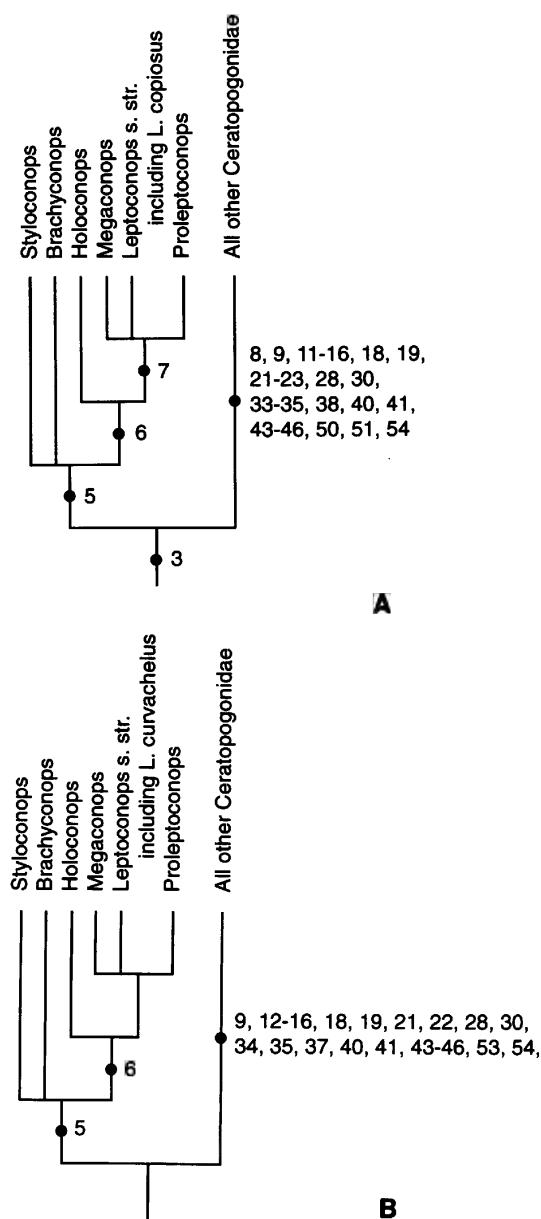


Fig. 10. Phylogenies of New Jersey amber Ceratopogonidae in relation to extant genera. Numbers refer to synapomorphies listed in table 1 and presented in figure 9. Presented synapomorphies are only those that could be seen in the fossil taxon or those (in the sister groups) that were absent in the fossil. Numbered synapomorphies for sister lineages are those found in that sister group or any lineage within that sister group. **A.** *Leptoconops copiosus*. **B.** *Leptoconops curvachelus*.

(Borkent et al., 1987) probably represent an apomorphic state further supporting the monophyly of that genus.

Heleageron grimaldii: The phylogenetic position of *Heleageron* was discussed by Borkent (1995). As such, its phylogenetic position is circumscribed by synapomorphies 16 and 28 (fig. 11B) and the genus may belong to any of a number of clades in this region of the cladogram.

The lack of a synapomorphy establishing *Heleageron* as a monophyletic group means that even though *H. arenatus* and *H. grimaldii* are the only included members, it is not certain that they are sister taxa.

Culicoides casei: Grogan and Szadziewski (1988) pointed out that they could not be certain of the placement of this species within *Culicoides* Latreille, and Borkent (1995) also was unsure about its phylogenetic position. The recognition here that there are no palisade setae on the first tarsomere of the hindleg (character 28) eliminates the possibility suggested by Grogan and Szadziewski (1988) that *C. casei* might actually be a member of *Ceratopogon* (fig. 12A). Furthermore, *C. casei* has a well-developed hindleg tibial spur and parameres that do not overlap (characters 30, 31), indicating that it does not belong within *Ceratopogon*.

As discussed by Borkent (1995), extant *Culicoides* are questionably monophyletic and, furthermore, the one character state which indicates this (character 27) is absent (or impossible to see) in nearly all fossil *Culicoides*. Consequently, the phylogenetic placement of all Cretaceous *Culicoides* within that genus is questionable (including *C. casei*). Nevertheless, all included Cretaceous species are similar morphologically and at present are best considered members of the genus. The available character states indicate that all are in a restricted area of the cladogram of genera of Ceratopogonidae (fig. 12A, B).

Culicoides bifidus: Available character states indicate that this species is reasonably placed in the current concept of Cretaceous *Culicoides* (fig. 12B). See discussion above under *C. casei* for further pertinent discussion.

Culicoides grandibocus: Because the single available specimen of this species was in poor condition, only a few character states could

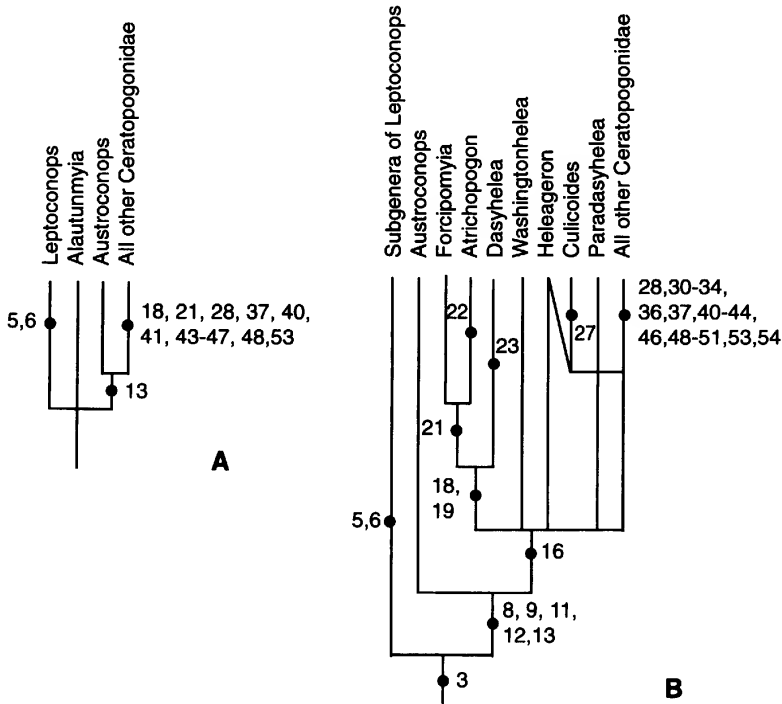


Fig. 11. Phylogenies of New Jersey amber Ceratopogonidae in relation to extant genera. For details see caption to figure 10. A. *Alautunmyia*. B. *Heleageron* (from Borkent, 1995).

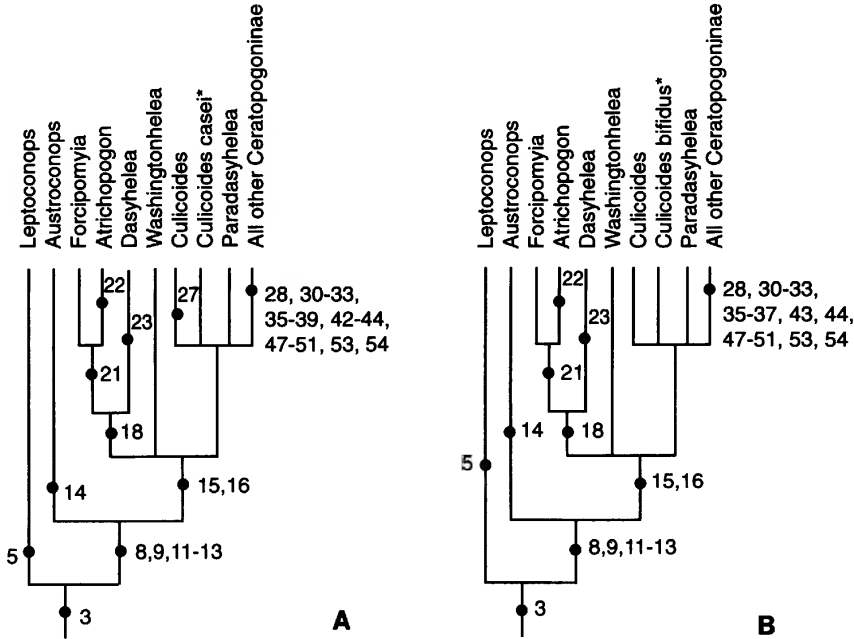


Fig. 12. Phylogenies of New Jersey amber Ceratopogonidae in relation to extant genera. For details see caption to figure 10. A. *Culicoides casei*. B. *Culicoides bifidus*.

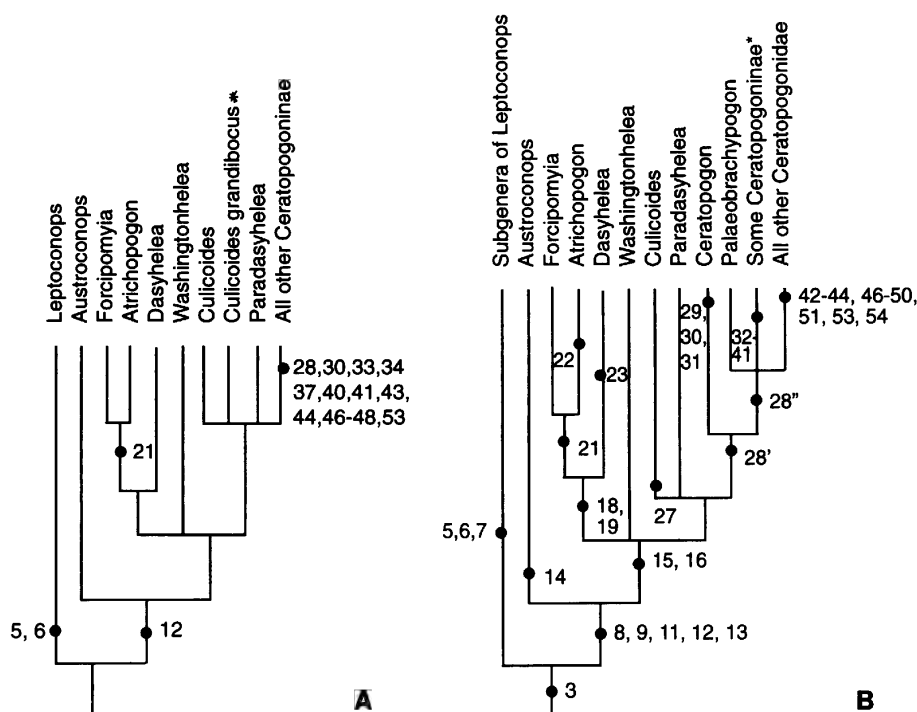


Fig. 13. Phylogenies of New Jersey amber Ceratopogonidae in relation to extant genera. For details see caption to figure 10. A. *Culicoides grandibocus*, * All other Cretaceous *Culicoides* are also in this phylogenetic position. B. *Palaeobrachypogon* (from Borkent, 1995), * refers to taxa listed in figure 9.

be scored (fig. 13A) and the evidence for its phylogenetic placement is poor. Nevertheless, the species is very similar to *C. filipalpis* and I have indicated its phylogenetic position accordingly. The presence of very elongate mouthparts may be a synapomorphy of the two species, indicating a sister group relationship (or possibly an ancestor/descendent relationship). However, mouthpart length is homoplastic in extant Ceratopogonidae, probably reflecting differences in food preferences, and this feature is probably a weak indicator of phylogenetic relationship.

Palaeobrachypogon remmi: The phylogenetic position of *Palaeobrachypogon* (fig. 13B) was discussed by Borkent (1995). It is unclear how the five included species (all Upper Cretaceous) are related to one another or whether they, in fact, form a monophyletic group.

CONCLUSIONS

Borkent (1995) pointed out that the Ceratopogonidae in the successively older Baltic

(Oligocene-Eocene), Canadian (Upper Cretaceous: Campanian), Taimyr (Upper Cretaceous: Coniacian-Santonian), and French (Upper Cretaceous: Cenomanian) ambers only include successively older lineages within the family. For example, a broad spectrum of lineages are present in Baltic amber, including taxa with synapomorphies 52" and 53" (fig. 9). No taxa with synapomorphy 42 are known from Cretaceous ambers, indicating that this lineage likely evolved and diversified between the Upper Cretaceous and the Eocene.

Four species (based on four specimens) were described or noted from French amber (Cenomanian) by Szadziewski and Schlüter (1992) who placed them in the genera *Leptoconops*, *Austroconops*, and *Atriculicoides*. These fossils are the oldest described Ceratopogonidae. They also represent only the very oldest lineages of Ceratopogonidae (see fig. 9; *Atriculicoides* is the extinct sister group of *Forcipomyia* + *Atrichopogon* + *Dasyhelea*). The slightly younger New Jersey amber *Culi-*

coides casei described by Grogan and Szadziowski (1988) was too poorly understood to be included in the analysis by Borkent (1995). These tentative results indicate that the lineage defined by synapomorphies 17" and 26 may have diversified between 83 and 99 million years ago (Borkent, 1995). The analysis here of New Jersey amber Ceratopogonidae, slightly younger than French amber, provides further resolution to this conclusion. The presence of synapomorphy 28" in *Palaeobrachypogon remmi* from New Jersey amber proves that members of that lineage were present during the Turonian (88–93.5 mya) and that all earlier clades must have arisen before that time. Furthermore, the presence of synapomorphy 28" in a taxon in Turonian New Jersey amber and its absence in ceratopogonids in Cenomanian French amber (although these admittedly included only a few specimens) may show that synapomorphy 28 evolved during the Cenomanian/Turonian period.

Borkent (1995) discussed the fact that none of the "extinct" genera of Cretaceous Ceratopogonidae exhibit autapomorphies, which would indicate that they were truly extinct lineages that left no descendants. All may be ancestral to extant groups and the results of the current analysis of New Jersey amber Ceratopogonidae confirm this pattern. The new genus *Alautunmyia*, known only from New Jersey amber, may in fact be ancestral to one of the most basal lineages of the Ceratopogonidae present today. As such, the Ceratopogonidae provide no evidence of an Upper Cretaceous extinction event.

The presence of only early lineages of Ceratopogonidae in Cretaceous fossil deposits

corresponds to that found in the Formicidae, where Upper Cretaceous ants represent the earliest lineages within the family (Wilson et al., 1967a, 1967b; Wilson, 1985, 1987). Of the two remaining taxa that have been described in detail from New Jersey amber, the Apidae belong to an extant bee genus that appears to be in a cladistically derived phylogenetic position (Michener and Grimaldi, 1988a, 1988b) and the Sciarioidea is of uncertain affinity (Grimaldi et al., 1989).

An important paleoecological inference can be made from this study of ancient midges. Crepet et al. (1992) described small hamamelidaceous flowers from the Late Cretaceous of New Jersey (there are about 80 taxa) and pointed out that the unknown insect pollinators would likewise need to be rather tiny to be effective pollinating agents. Some of the Ceratopogonidae described here would be reasonable candidates as pollinators not only because they are small, but some modern representatives of early lineages of Ceratopogonidae (i.e., *Forcipomyia*, *Atrichopogon*, *Dasyhelea*; see fig. 9) are known to be important pollinators of extant, small-flowered angiosperms (i.e., Young, 1983). In addition, many extant ceratopogonids are abundant on plants with small flowers, e.g., mango (*Mangifera indica*), buffaloberry (*Shepherdia canadensis*; personal obs.), although their importance as pollinators on these has not been investigated. This suggests that the Cretaceous representatives of the family may have been important pollinators as well. Indeed, these Cretaceous ceratopogonids may have played key roles in the radiation of angiosperms.

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